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遗迹化石：探索生物与环境相互作用的重要信息载体*

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提要 遗迹化石是地质历史时期生物在沉积物表面和内部所留下的生命活动记录。遗迹化石不仅与生物种类和生活习性密切相关，还受到环境因子和沉积介质的影响和控制。地质地史时期的软躯体生物很难保存为化石，而它们生命活动的行为习性都烙印在了遗迹化石里。因此，遗迹化石成为探索生物与环境相互作用的重要信息载体，在重建古环境和古生态、探索早期生命演化和理解重大地质转折期底栖生态系对极端环境事件的响应上具有重要意义。本文聚焦于近年来这三大方向遗迹学方面的研究进展，并对将来遗迹学的发展方向进行了展望。

关键词 遗迹化石 生物与环境 早期生命 古生态 生物复苏

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Trace fossil: a significant agent for exploring organism-environment interactions

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Abstract Trace fossils record the behavioral characteristics of ancient organisms, and their preservations reflect the intimate interaction between organisms' ethology, habitable substrates, and their living environments. In particular, soft-bodied organisms usually are difficult to be preserved in the fossil records, but their behaviors can be preserved as

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trace fossils. Thus, trace fossils are pivotal in reconstructing palaeoenvironmental and palaeoecological interpretations, deciphering the early evolution of life and the infaunal responses to environmental extremes during mass extinctions. This paper focuses on the advancement of the above mentioned ichnological research topics during the past ten years, and puts forward potential directions in future ichnological studies.

Key words trace fossil, organism and environment, early life, palaeoecology, biotic recovery

1 前 言

遗迹化石是地质历史时期保存在沉积物表面和内部的生命活动遗迹。与实体化石不同，遗迹化石记录了生物的行为学特征。遗迹学发展从“藻类时代”到“现代遗迹学时代”，经历了漫长的发展历程(范若颖、龚一鸣，2014)。20 世纪 50 年代 Seilacher 和 Häntzschel 在遗迹学领域做出的开创性工作，使得遗迹学成为一门真正的学科(Seilacher, 1967; Häntzschel, 1975)，并构成了古生物学、生态学和沉积学之间重要的交叉学科。遗迹化石的保存，不仅跟生物的种类和生活习性密切相关，还与生物生活的环境条件(如底质氧含量、水动力条件、盐度和营养物质的类型和多寡等)和沉积底质条件(如软底、硬底、固底、汤底和木底等)紧密相关。这使得遗迹化石不同于实体化石：1)遗迹化石记录了生物的行为学特征；2)同一生物可营造不同的生物遗迹类型(一物多迹)；3)相同类型的生物遗迹可由不同生物所形成(造迹生物的非限定性)；4)多个生物可能共同形成一种生物遗迹(多物一迹)；5)造迹生物常为软躯体生物，也可由具硬体的生物形成；6)遗迹化石常保存在无实体化石保存的哑地层中；7)同一遗迹属可能因底质不同而呈现不同形态；8)大多数遗迹化石常常有较长的时间延续；9)特定的遗迹化石组合常具有窄的环境分布；10)遗迹化石多为原地埋藏，很少被搬运(Bromley, 1996；杨式溥等，2004; Buatois and Mángano, 2011; Minter *et al*., 2016)。基于遗迹化石的这些特点及与环境条件之间的紧密联系，遗迹学成为探索深时生物与环境相互作用的重要媒介，在重塑古环境和古生态、探索地球早期生命演化、解读重大地质转折期的生态系复苏以及石油与天然气地质等中都有着非常重要的应用。笔者聚焦于近 10 余年来遗迹学在前三个方面所取得的新进展、新发现，并做了系统梳理和总结，最后对未来遗迹学发展的新方向进行了展望。遗迹学在石油与天然气地质中的应用涉及范围较广，将另外撰文详细论述。

2 遗迹化石与古环境和古生态再造

利用遗迹化石重塑古环境和古生态，一直是遗迹学的主要研究内容，也是历届遗迹组构国际研讨会和国际遗迹学大会的重要议题之一(齐永安等，2008；张立军等，2015；范若颖、龚一鸣，2017；牛永斌等，2019)。遗迹化石是生物行为学的最直接证据，能为探寻古代生物的生态习性和觅食、繁殖策略提供实证，并在环境条件发生变化时产生相应遗迹学响应。例如，新疆上泥盆统洪古勒楞组中发现的一类辐射圆盘状遗迹，与现今日本海域附近雄性河豚因求偶在海底沙面建造的形态精美辐射状遗迹非常相似(图 1-A，1-B; Zong and Gong, 2018)。这一研究将生物的求偶行为追溯到 360 Ma 前的泥盆纪，并为解答生物求偶和性选择行为的演化提供了重要古生物学实例。此外，古代鱼类的觅食过程，也被遗迹化石所记录，并形成了特定的鱼类觅食迹 *Osculichnus* (图 1-C; Fan *et al*., 2019)。这一研究为利用遗迹学理解古代鱼类的觅食行为提供了可能性。此外，Luo 等(2020a)等人最近报道了位于南悉尼盆地早二叠世 Snapper Point 组中一种新的遗迹组构(图 1-D)。通过对野外地层沉积学和遗迹学的观察和测量，发现这类 *Parahaentzschelinia* 遗迹组构代表了在三角洲环境内生底栖双壳类对快速沉积过程的密切响应。沉积物快速堆积使得造迹生物不断调整其和沉积物–水界面之间的位置，造成遗迹化石不断往上迁移的均衡构造(equilibrium structure)。当时盛行的早二叠世季风性气候很可能形成河流季节性洪涝，大量沉积物被河流携带并快速堆积

在三角洲环境。根据 *Parahaentzschelinia* 遗迹组构叠覆序列的高度和这类双壳类造迹生物的最大生活史, 恢复了当时三角洲沉积速率为 0.24 cm/y (Luo *et al*., 2020a)。

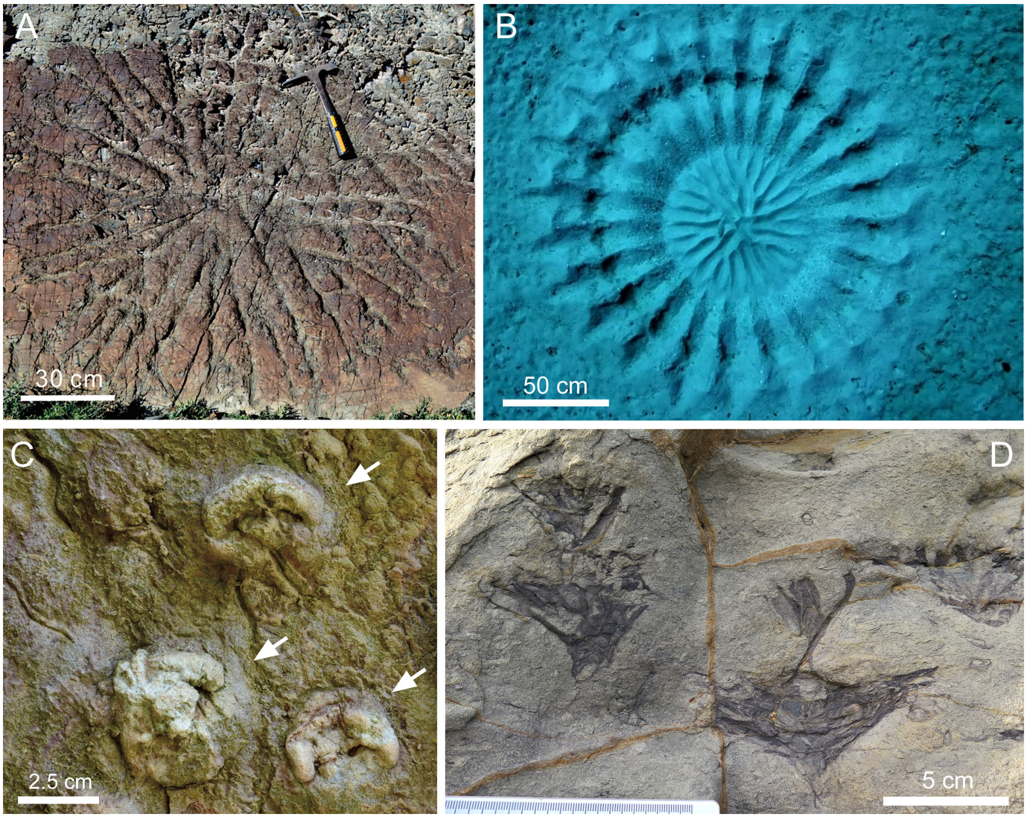

图 1　新发现代表不同生态学行为的遗迹化石示例

Fig. 1　Newly discovered trace fossils representing different ecological behaviours

A, 新疆晚泥盆世洪古勒楞组中发现的求偶迹与现代日本海域河豚求偶构造(**B**)的比较; **C**, 湖北武汉地区晚泥盆世五通组砂岩中发现的鱼类觅食留下的吻捕迹 *Osculichnus* (引自 Fan *et al*., 2019); **D**, 南悉尼盆地早二叠世 Snapper Point 组中发现的一类新的 *Parahaentzechelinia* 遗迹组构。

A, Courtship trace fossil found from the Upper Devonian Hongguleleng Formation of Western Junggar in Xinjiang Province (from Zong and Gong, 2018). **B**, radiated sand bedform on seafloor created by *Torquigener albomaculosus* in Japan Sea. **C**, Fish hunting trace *Osculichnus* on sole surface of sandstone, Upper Devonian Wutong Formation, Wuhan of Hubei Province (from Fan *et al*., 2019). **D**, funnel-shaped trace fossil *Parahaentzschelinia* isp. forming stacked ichnofabric, Lower Permian Snapper Point Formation of southern Sydney Basin, Australia (from Luo *et al*., 2020a).

利用遗迹化石指示沉积环境的氧化还原条件, 一直是众多遗迹学家关注的焦点(如: Bromley and Ekdale, 1984; Martin, 2004; Savrda, 2007)。近年的研究表明, 某些特定遗迹化石对沉积底质氧化还原的指向性, 可能并未如前人理解的那样简单。例如, 对丛藻迹(*Chondrites*)的研究, 因其造迹生物常被认为是一类生活于氧化还原界面之下, 营化学共栖(chemosymbiosis)的蠕虫动物所造成(Seilacher, 1990; Fu, 1991), *Chondrites* 的出现常被用来指示缺氧和贫氧的沉积环境(Bromely and Ekdale, 1984; Ekdale, 1992; 杨式溥等, 2004)。最近的研究表明, 这种遗迹化石不仅造迹生物多样, 而且广泛分布于浅水至深水环境(Baucon *et al*., 2020)。此外, 无生物扰动的泥岩沉积, 通常被认为沉积于缺氧的环境条件(Ekdale and Mason, 1988; Kaiho, 1994; Poulson *et al*., 2006; Savrda, 2007)。然而, Dashtgard 和 MacEachern (2016)对白垩纪 Abian 期砂质泥岩的遗迹学和地球化学研究表明, 无生物扰动泥岩沉积形成于有氧底质水条件, 缺乏生物扰动是由于底层水中氧含量相对较低(溶解氧在 2−5 mg/L), 不足以支持宏体造迹生物的新陈代谢并在沉积物中形成生物扰动(Dashtgard and MacEachern, 2016)。这一研究提醒我们, 可能地史时期并非所有泥岩沉积都代表了缺氧条件下的沉积产物。

3 遗迹化石与早期生命演化

早期生命，特别是寒武纪以前的宏体生物，几乎都是软体。这些生物因缺乏坚硬外壳或内骨骼，很难在地层记录中保存为化石，但他们的生命活动却能保存为生物遗迹。基于此，遗迹化石为探索早期生命的演化过程打开了窗口。

分子钟测算认为，最早的后生动物可追溯至拉伸纪(Tonian, 1000−720 Ma)，两侧对称动物的出现和分化时间则是在成冰纪或埃迪卡拉纪(Erwin *et al*., 2011; Reis *et al*., 2015)。然而，有确切化石记录的两侧对称动物更可能出现在埃迪卡拉纪晚期。这些记录包括很少量的实体化石和遗迹化石。虽然有部分学者报道的遗迹化石记录似乎支持动物出现的时间可能在12亿年前(Rasmussen *et al*., 2002)，但后续研究更倾向于认为这些记录为假化石(Conway Morris, 2002; Jensen, 2003)。乌拉圭Tacuarí组与冰期沉积有关的浅海相地层中的遗迹学研究认为两侧对称后生动物的化石可延续至埃迪卡拉纪中期(~585 Ma, Pecoits *et al*., 2012)。这些保存在粉砂岩顶面和底面浅表层二叶型遗迹由两列平行凹槽和分隔凹槽的脊状突起所组成。保存较好的标本有串珠状的回填构造，并在潜穴边缘(凹槽处)保存有细微的椭圆形凹坑(Pecoits *et al*., 2012)。上述遗迹学特征被解释为具有类似足状附肢的两侧对称动物在沉积物内部觅食所造成。尽管这一遗迹学证据记录的两侧对称动物出现时间与分子钟推算时间相吻合，很遗憾的是，其他研究人员指出这段地层的时代为石炭−二叠纪，而非埃迪卡拉纪中期(Gaucher *et al*., 2013)。因此，对于埃迪卡拉纪中期以前两侧对称动物的化石记录，目前仍无可靠报道。

近年来，湖北三峡地区灯影组石板滩段(551–541 Ma)中发现和保存大量精美的遗迹化石(Chen *et al*., 2013, 2018, 2019)，证明两侧对称动物至少在埃迪卡拉纪晚期出现。比如，报道中发现了一类新遗迹属(*Lamonte*)由两列平行、重复性序列状行迹。遗迹中每个单列保存了多个可重复的小凹陷，在岩层底面保存的遗迹则表现为一系列的凸起。这些重要特征指示了这些遗迹为具有足状附肢的动物在沉积物表面爬行所造成。更重要的是，多条这类遗迹在相互交切时，交切部位特征清晰可见，行迹未受到明显扰动。这些证据表明，这些遗迹为具有足状附肢，并利用附肢支撑起身体在沉积物表面形成爬行迹，而非生物紧贴沉积物表面或深入沉积内部蠕动所形成(Chen *et al*., 2018)。这些遗迹学证据将具有足状附肢两侧对称动物的记录追溯至寒武纪之前的埃迪卡拉纪晚期，并表明在这一时期，造迹生物的行为具备了相当高的复杂性。附肢作为专门的运动器官，使动物的运动能力得到极大提高，其出现是动物演化史上的重大事件。因此，这一新的发现也被生动形象地比喻为“虫子的一小步，动物演化史上的一大步” (朱茂炎, 2018)。最近报道的一类两侧对称生物及其死亡迹(临终遗迹，mortichnia)的共同保存，进一步将两侧和分节动物的出现时间提前到了埃迪卡拉纪晚期(华洪, 2019; Chen *et al*., 2019)。这一研究也表明，泛节肢动物的祖先至少可追溯至5.5亿年前。无独有偶，最近在全球埃迪卡拉纪金钉子剖面地层下部，也发现了一类新的两侧对称动物 *Ikaria wariootia* 及其造成的遗迹 *Helminthoidichnites* (Evans et *al*., 2020)。上述研究进一步强化了两侧对称动物在埃迪卡拉纪晚期就已经分化出现的观点。

此外，埃迪卡拉纪晚期生物的生活方式很可能与微生物席的发育密切相关。以蓝细菌为主的微生物席建造，在光合作用下可产生大量氧气，使得藻席附近构成富氧环境，为宏体动物的生存和生命活动创造了有利条件(Gingras *et al*., 2011)。这一时期造迹生物可以在有藻席发育的表层和浅表层自由活动。而沉积物深部空间氧含量仍很低，造迹生物还无法触及。埃迪卡拉纪微生物席底质的广泛发育，为早期宏体生物的生命活动和演化提供了重要物质基础(Xiao *et al*., 2019)。

4 遗迹化石探索重大地质转折期生态系复苏

重大地质转折期的生态系复苏是地质学家和古生物学家长期关注的热点和前沿。特别是显生

宙 5 次生物大灭绝后的生态系复苏, 一直受到古生物学家, 古气候学家和地球化学家的高度关注。对生物复苏的过程和时限的探索, 以往研究多从实体化石入手, 对遗迹化石研究不多。自 Ekdale 和 Bromley (1984) 利用遗迹化石探索造迹生物在白垩纪末期大灭绝后对极端环境的响应后, 越来越多的研究者从研究遗迹化石角度探讨和理解大灭绝后底栖生态系对极端环境的响应过程和机制, 并将研究聚焦于二叠纪−三叠纪之交的遗迹学记录(赵小明、童金南, 2010; Twitchett and Wginall, 1996; Twitchett, 1999; Pruss and Bottjer, 2004; Cao and Zheng, 2009; Fraiser and Bottjer, 2009; Knaust, 2010; Zonneveld *et al*., 2010; Chen *et al*., 2011; Hofmann *et al*., 2011; Luo and Chen, 2014; Luo *et al*., 2016, 2017, 2019a, 2019b, 2020; Feng *et al*., 2017, 2018, 2019; Zhang *et al*., 2017, 2018, 2019, 2020)。最近两届遗迹组构国际研讨会, 也出现对这一热点方向的专题讨论(范若颖、龚一鸣, 2017; 牛永斌等, 2019)。

最近 30 年的研究中, 为评估底栖生物的复苏过程和级别, 各国学者应用了诸多遗迹学指标来综合评价底栖生物的复苏级别(Taylor and Goldring, 1993; Twitchett and Wignall, 1996; Miller and Smail, 1997; Miller, 2003; Buatois and Mángano, 2013; Buatois *et al*., 2017), 从而合理解释生态系复苏的时空模式。这些常用的遗迹学指标包括遗迹化石分异度(ichnodiversity)、遗迹悬殊度(也译作遗迹歧异度, ichnodisparity, 黄冰, 2012; 刘梦瑶、张立军, 2018)、生物扰动指数/遗迹组构指数(bioturbation index / ichonfabric index)、层面生物扰动指数(bedding plane bioturbation index)、潜穴大小、关键遗迹化石属的出现、阶层(tiering)分布和遗迹化石复杂度(trace fossil complexity)等。这些指标的综合运用, 可合理评估底栖生物的复苏级别。然而, 这些指标的具体意义、影响因素和可靠性, 仍存在一些不确定性, 并深刻影响将来合理使用遗迹学记录正确解读生态系复苏的过程和时限。Luo 等(2020b)基于二叠纪−三叠纪之交的遗迹化石研究, 对反映生态系复苏的所有遗迹学指标进行了系统梳理和总结, 并对每一个遗迹学指标的内涵和外延进行了界定。该研究筛选出了可以合理应用的遗迹学指标, 并给出这些指标的使用注意事项(如遗迹学多样性、生物扰动指数、阶层分布、潜穴大小等); 同时也摒弃了一些遗迹学指标(如层面生物扰动指数)。这一研究为今后合理利用遗迹学指标评估生态系复苏奠定了良好的基础。

利用遗迹化石大数据研究, 在阐明二叠纪末生物大灭绝事件之后的生物复苏上也取得了一定进展。Luo 等(2021)整合了全球二叠纪−三叠纪之交的所有遗迹学记录, 基于严格的遗迹化石鉴定和评估, 再现了全球遗迹化石属分异度和悬殊度(ichnodisparity)变化曲线(图 2-A, 2-B)。这一研究发现遗迹化石分异度与实体化石之间有明显解耦现象(图 2-C), 在大灭绝事件后, 实体化石多样性出现了急剧下降, 而遗迹化石分异度不但没有明显降低, 还保持了与大灭绝事件前的分异度水平(图 2-A)。对不同时段遗迹属特征分析得到的遗迹阶层组成表明, 早三叠世不同时期, 遗迹化石均以浅阶层或表层遗迹占主导, 多数造迹生物只在沉积物表层和浅表层活动, 而在大灭绝事件前(如吴家坪期和长兴期)和生态系完全复苏之后的中三叠世各时期, 深阶层遗迹的占比明显更多(Luo *et al*., 2021)。这一现象与早三叠世微生物岩的发育形成很好的对比关系。这一研究指出大灭绝后微生物席的大量发育, 很可能为浅阶层遗迹的保存创造了良好条件, 也一定程度反映出早三叠世混合层缺失而导致的低生物扰动特性(Hofmann *et al*., 2015)。最近的研究也表明, 在大灭绝事件后微生物席生态系的发育为崩溃生态系造迹生物的生存提供了重要驱动(Luo *et al*., 2019)。

在比较历次大灭绝事件生态系复苏的过程和模式上, 遗迹化石组合及其反映复苏的遗迹学指数亦展现出不同的变化特征(张立军等, 2015)。比如, 二叠纪末期大灭绝事件后, 整个生态系复苏延续了相当长时间。反映生态系复苏的各项遗迹化石指数表明, 整个浅海生态系直到中三叠世早期才完全复苏, 整个复苏经历了 5 Ma (Chen *et al*., 2011; Luo *et al*., 2016, 2019a, 2019b; Feng *et al*., 2018; Stachacz and Matysik, 2020)。造迹生物的响应结果显示的复苏时限与实体化石研究显示的结果吻合(Chen and Benton, 2012; Benton *et al*., 2013), 这一延迟性复苏也深刻地反映了二叠纪晚期−早三叠世这一时期极端环境变化的强度和延

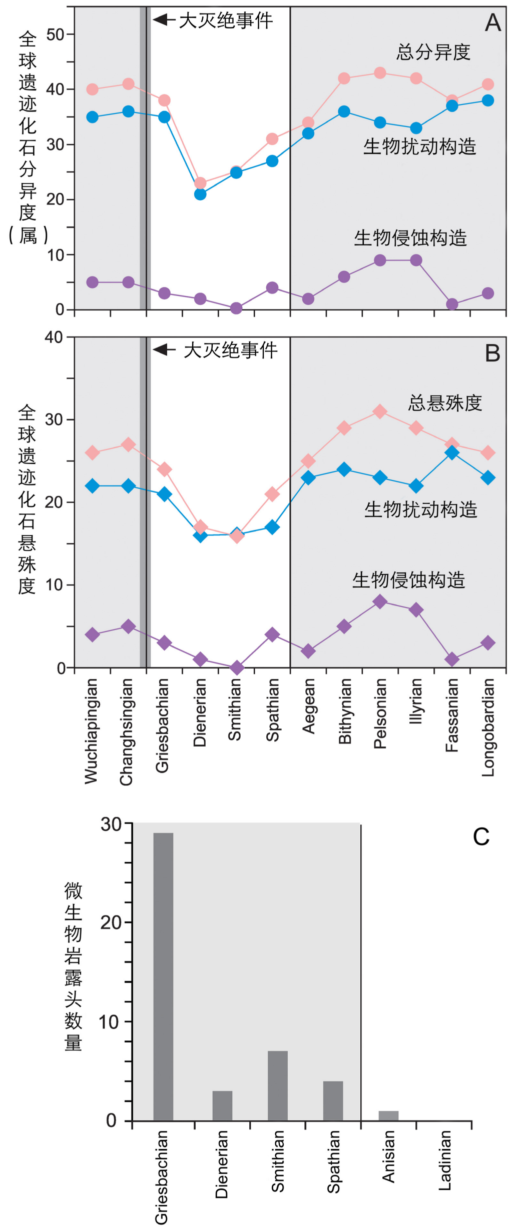

图 2 晚二叠世至中三叠世不同时期全球遗迹化石分异度(**A**)和悬殊度曲线(**B**)及其与早三叠世微生物岩相对丰度(**C**)的比较(修改自 Luo *et al*., 2021)

Fig. 2 **A**, Trend of global ichnodiverstiy from late Permian to Middle Triassic. **B**, Trend of global ichnodisparity from late Permian to Middle Triassic. **C**, Relative abundance of microbialites from Lower to Middle Triassic (all figures modified from Luo *et al*., 2021)

续时限之久。与这一时期遗迹学响应产生鲜明对比的是白垩纪末期大灭绝事件后的遗迹学响应。Rodríguez-Tovar 等(2006, 2011, 2020)对法国西南部、西班牙北部以及墨西哥东南部尤卡坦半岛等地白垩纪–古近纪地层中遗迹化石的系统研究发现，反映生态系复苏的多个遗迹学指标，如遗迹化石分异度、潜穴大小、阶层等在灭绝界线之上很快就恢复到灭绝前水平,这一遗迹学响应反映出复苏时限很短，仅为 70 万年(Rodríguez-Tovar *et al*., 2020)。这一结果表明白垩纪末期大灭绝事件后海洋生态环境的转变是一个非常迅速的过程。另一方面，因白垩纪末大灭绝事件本身的强度较弱(沈树忠、张华, 2017)，撞击事件对环境变化的影响也有限，造成其后生态系的快速复苏。

5 研究展望

新技术、新方法的发展和在遗迹学中的应用,已成为近几届遗迹组构国际研讨会的常规议题之一(齐永安等, 2008; 张立军等, 2015; 范若颖、龚一鸣, 2017; 牛永斌等, 2019)，并将在未来遗迹学发展上发挥重要推动作用。最近 10 多年来, Micro-CT 以及同步辐射显微断层成像(Synchrotron microtomography)的发展，在精细解读重要化石内部解剖学结构上，展现出巨大潜力，并助力在探索早期生命演化和揭示重大地史转折期生物与环境相互作用机制中取得了重要进展(Yin *et al*., 2015; Bao *et al*., 2019)。这些技术也逐渐用于遗迹学研究中。例如，Kiel 等(2010, 2013)等人在渐新世鲸鱼化石骨骼中发现了一类微小的钻孔遗迹。利用 Micro-CT 扫描技术对这类遗迹进一步分析,发现这类钻孔遗迹与现今才发现的一类生活于深海的环节动物钻孔类似，并将这类生物的演化历史追溯至渐新世，而鲸类在渐新世的大辐射过程很可能促进了这类啃食和消化动物骨骼的环节动物的演化(Kiel *et al*., 2010)。

在研究方向上，重大地质转折期的遗迹学响应将会是目前和今后研究的热点。这包括大灭绝事件后造迹生物对极端环境的响应过程和机制研究，还包括诸如前寒武纪早期生命演化时期、寒武纪生命大爆发和奥陶纪生物大辐射期遗迹学的响应等。这些研究一方面依赖于扎实掌握遗迹化石系统分类的理论基础并对其合理运用，另一方面依赖于高精度生物地层学和年代地层学的发展和完善。建立遗迹化石大数据，并引入统计学的分析方法对深时重大地史转折期遗迹化石分异

度、悬殊度(disparity)和造迹生物对生态空间利用程度的时空变化, 将为进一步理解生物与环境的协同演化机制提供重要线索(Buatois *et al*., 2016, 2020; Minter *et al*., 2017; Zhang *et al*., 2019; Luo *et al*., 2021)。区分生物遗迹和非生物遗迹也是摆在前寒武纪遗迹学研究上的难点。微生物席广泛发育的前寒武纪, 微生物席沉积构造往往因受到波浪、潮汐和沉积后期物理作用改造, 产生不同形态的层面构造而形似实体化石或是遗迹化石(Mariotti *et al*., 2016; Nelson and Smith, 2019; McMenamin, 2020; Warren *et al*., 2020)。这使得仅仅依赖于宏观形态特征为标准鉴定和判断埃迪卡拉纪地层中的遗迹甚至是实体化石有时显得异常困难, 有待于其他指标(如地球化学特征)综合运用区分这些微生物沉积构造和遗迹化石。另外值得一提的是, 新遗迹学(Neoichnology)研究的深入, 也将是今后遗迹学领域的一个重要方向。虽然目前已有研究对现代海滩滨岸环境潜穴形态, 分布特征和造迹生物的生态习性等进行了初步研究(Dashtgard, 2011; Wang *et al*., 2019), 但对于陆架区浪基面以下, 以及风暴浪基面附近现代生物的潜穴行为和形成潜穴形态特征, 中国目前这方面研究仍非常欠缺。揭开现代海洋浅水陆架区和深水盆地相区生物的造迹行为和潜穴组合特征, 并对其进行原位生物潜穴行为的观察研究将为进一步理解遗迹相、遗迹化石的形态功能分析和古环境解释提供重要佐证。

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